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New species and new records of *Reteporella* (Bryozoa: Cheilostomatida) from Greenland waters

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Abstract

New species and new records of the cheilostome bryozoan family Phidoloporidae are reported from the poorly studied shelf and continental slope of Greenland. *Reteporella vitta* **n. sp.** differs from congeners in the shape and size of fenestrulae, the size of autozooids and their arrangement within the colony, features of the orificial complex, including the indistinctly denticulate distal rim, shape of the condyles and height of the peristome, as well as the shape and location of the suboral avicularium, and the morphology of the ovicell. *Reteporella obscura* **n. sp.** differs from other *Reteporella* species in a unique combination of the following characters: colony surface texture, shape of orifice and condyles, shape of the suboral avicularium, and the morphology of the ovicell. Other specimens of *Reteporella* from Greenland were identified as *R. watersi* (Nordgaard, 1907), firstly recorded in southern and western parts of the study area, and as *R. grimaldii* (Jullien, 1903) and *R. beaniana* (King, 1846), previously known only from some localities of western and eastern Greenland and recorded abundantly in 2016. *Reteporella watersi* specimens from Greenland differ from conspecific material from the Faroe Islands in lacking oral spines and in the size of zooidal characters.

Key words: Taxonomy, Phidoloporidae, new species, Greenlandic shelf and slope, northwestern Atlantic

Introduction

Phidoloporidae Gabb & Horn, 1862 is one of the most diverse families among bryozoans in the World Ocean (Pagès-Escolà *et al*. 2020), and *Reteporella* Busk, 1884 is the largest genus in the family. *Reteporella* has been reported from the Arctic to the tropics (Bock & Gordon 2021) and currently includes 132 species. Diagnostic features for the genus include a lacy colony, a well-developed peristome with open or closed asymmetric lobes (in the latter case, the sinus becomes an asymmetrically placed spiramen), and an elongate fissure in the ovicell. Adventitious avicularia are also usually numerous on one or both surfaces of the colony (Busk 1884).

Despite its high species richness, *Reteporella* is poorly represented in the Arctic region, with only six species reported to date, namely: *R. beaniana* (King, 1846), *R. couchii* (Hincks, 1878), *R. grimaldii* (Jullien, 1903), *R. incognita* (Hayward & Ryland, 1996), *R. rara* (Jullien in Jullien & Calvet, 1903), and *R. watersi* (Nordgaard, 1907) (Denisenko *et al.* 2016). Of these, *R. grimaldii* and *R. beaniana* allegedly have a wide geographical occurrence. The eastern distributional boundary of the first nominal species is the deep northern part of the Kara Sea; *R. beaniana* is known from the western shelf edge of the Barents Sea (Kluge 1962; Denisenko 1990) and in Greenland waters (Smitt 1968; Levinsen 1916; Hansen 1962). However, the Arctic specimens, collected only from a few localities, have not yet been analyzed using scanning electron microscopy (SEM). The distribution is restricted to more southerly areas of the Arctic's Atlantic sector for three of these species. *Reteporella rara* and *R. couchii*, initially described from the Azores in the central North Atlantic (Jullien & Calvet 1903) and Great Britain (Hayward & Ryland 1996), respectively, were also reported from around the Faroe Archipelago (Hayward 1994; Hayward & Ryland 1996; Klitgaard 1995), from which *R. incognita* was also originally described but from deeper waters (Hayward & Ryland 1996). The latter species, *R. watersi*, is widely distributed in the Arctic. It has been reported from the northern part of the Greenland Sea (Levinsen 1916; Koltun 1964; Kuklinski 2009), the Arctic basin north of the Franz-Josef Land Archipelago (Kluge 1962), and around the Faroe Archipelago (Hayward 1994; Denisenko *et al.* 2016). In the high

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Arctic, it occurs only sporadically, while it was most frequently recorded in the Faroe Islands area (Denisenko *et al.* 2016), and in Iceland waters (Hayward *et al.* 2020). As for *Reteporella* from the southern and western parts of the Greenland shelf and continental slope, only two species (i.e. *R. beaniana* and *R. grimaldii*) have been reported before the present study (Smitt 1867; Levinsen 1916; Hansen 1962).

Among all listed *Reteporella* species, only *R. watersi* and *R. rara* have a rough, dimpled texture on the frontal surface of autozooids and the abfrontal surface of the colony (Nordgaard 1907; Jullien & Calvet 1903). In 2016, several *Reteporella* specimens with similar texture were collected at sublittoral and bathyal depths in areas SE, SW, and NW of Greenland.

The aim of this study is to determine their taxonomic identity based on comparisons with related taxa, and to record the distribution of *Reteporella* species in Greenland waters.

Material and methods

Specimens of *Reteporella* were collected during cruises of the MT *Paamiut* in June–July 2016. *Reteporella grimaldii* was recorded at 16 stations, and *R. beaniana* at 49 stations at depths between 63–608 m and 89–563 m, respectively (Fig. 1).

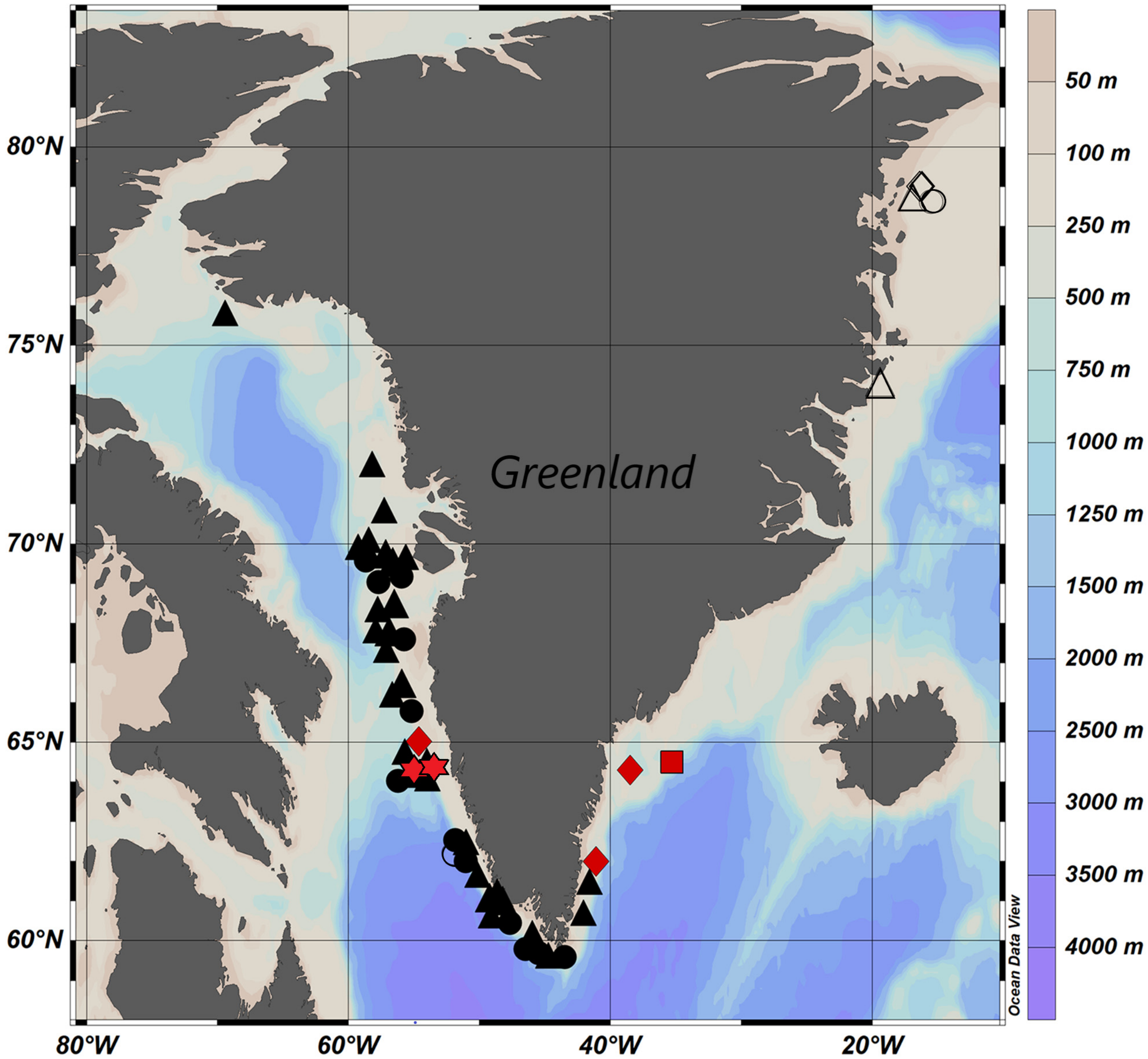

FIGURE 1. Occurrence of *Reteporella* species in Greenland waters. Symbols: triangle—*R. beaniana*; circle—*R. grimaldii*; star—*R. obscura* **n. sp.**; rhomb—*R. watersi*; square—*R. vitta* **n.sp.**. Empty symbols: literature information; full symbols: material newly collected in 2016.

Reteporella obscura **n. sp.** was found at two stations (Stn 2016_PA_2_151; 64.52786668° N, -54.7776999791463° W; and Stn 2016_PA_1_16; 64.35196667° N; -53.8765166600545° W; bottom water temperature (T) 1.575–3.934°C) from the lower sublittoral zone at 165–277 m depths (Fig. 1).

Reteporella vitta **n. sp.** was found at a single station (Stn 2016_PA_5_58; 64.8872833251953° N, –34.5760166803996° W; T 3.24°C) in the upper bathyal zone at 948 m depth (Fig. 1).

Reteporella watersi was recorded at three stations (Stn 2016_PA_1_22; 64.5355499903361° N; –55.1436500072479° W; 563 m; T 4.12°C; Stn 2016_PA_4_40; 61,9967333475749° N, –41,0106666664283° W; 234 m; T 3.9°C; and Stn 2016_PA_5_93; 64,1297000010808° N, –38,8902166366577° W; 320 m; T 4.137°C) (Fig. 1).

All specimens were initially fixed in 4% formaldehyde and later transferred to 70% ethanol. Several colony fragments were immersed in a sodium hypochlorite solution to remove the cuticles and soft parts, followed by examination under a stereomicroscope. Selected fragments were coated with platinum, and imaged with a QUANTA 250 (FEI) SEM at the Zoological Institute of the Russian Academy of Sciences. Measurements were taken from SEM images using the software ImageJ (Schneider *et al.* 2012). Measurements are presented in millimeters in the text and Tables 1–3; scale bars in the figures are indicated in micrometers. Sample sizes for measurements ranged from 5 to 30 (N).

The holotypes of *R. obscura* **n. sp.** and *R. vitta* **n. sp.,** all specimens of *R. watersi*, and some specimens of *R. beaniana* and *R. grimaldii* are deposited in the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) in Saint Petersburg.

Systematic account

Class Gymnolaemata Allman, 1856

Order Cheilostomatida Busk, 1852

Family Phidoloporidae Gabb & Horn, 1862

Genus *Reteporella* Busk, 1884

Type species: *Reteporella flabellata* Busk, 1884

Reteporella obscura n. sp.

(Fig. 2; Table 1)

Material examined. Holotype: ZIN 1/50742, one colony; Stn 2016_PA_2_151 (64.52786668° N, -54.7776999791463° W; 277 m; T 3.934°C); collected by BEAMTRAWL, MT *Paamiut*, fish-shrimp trawl assessment survey. July 2016.

Paratype: ZIN 2/50747; colony fragment; Stn 2016_PA_1_16 (64.35196667° N; -53.8765166600545° W; 165 m; T 1.575°C); collected by BEAMTRAWL, MT *Paamiut*, fish-shrimp trawl assessment survey. July 2016.

Diagnosis. Colony reticulate, broadly fan-shaped; fenestrulae large; different levels of granulation on frontal and abfrontal surfaces. Trabeculae of variable length, with 2–3 series of alternating zooids, doubling at bifurcations. Zooids flat, with 3–5 large marginal pores; marginal zooids near fenestrulae with 5–6 marginal pores. Orifice semicircular, approximately as wide as long with rounded condyles and slightly prominent proximal edge; distal rim smooth with a well-developed row of denticles in its lower part. Spines paired, one on each side of orifice at about mid-length; peristome asymmetric with a widely open pseudosinus; larger lobe with a small circular avicularium directed terminally-proximally relative to the zooidal surface; rostrum finely toothed, crossbar complete, columella absent, cystid invisible, mandible edge raised. Frontal avicularia sporadic, oval and relatively small, crossbar complete, columella absent, palate forming a more or less developed shelf, distal uncalcified area semicircular. Abfrontal avicularia rare, circular, distal part raised with fine denticulation. Ovicells longer than wide with long fissure, and relatively narrow labellum.

Etymology. Latin "*obscura*" (unclear), alluding to the possibility of misidentification with closely related species of *Reteporella*.

Description. The colony is 40–50 mm high, broadly fan-shaped. The fenestrulae are mainly oval, twice as long as wide, commonly 1.1 x 0.53 mm (Fig. 2A, B; Table 1). The trabeculae (0.85 x 1.05 mm) consisting of two to three alternating, longitudinal series of autozooids, doubled at points of trabecular bifurcations (Fig. 2A). The abfrontal surface of the colony is densely and finely granulated, covered by flat kenozooids clearly delimited by vibices, and with rare round avicularia (Fig. 2B). One horn-shaped kenozooid (about 0.5 mm in length) with a rounded avicularium was observed (Fig. 2A, C, G). The granulation on the frontal side is comparatively coarser but less dense than that on the abfrontal surface (Fig. 2A, B).

Autozooids are elongate hexagonal, delimited by mainly straight edges, and occasionally by sutures, obscured by later calcification; autozooids size is about 0.49 x 0.275 mm, but width and length vary considerably especially in areas of bifurcation (Fig. 2D, J; Table 1). The autozooids have few (2–3) large, distinct marginal pores but zooids located near fenestrulae have an additional row of 5–6 pores near the external edge (Fig. 2D, J).

TABLE 1. Measurements (in mm) of *Reteporella obscura* **n. sp.** (holotype). SD, standard deviation; N, number of measurements.

Character measured	Mean ± SD	Range	N
No. zooid rows between fenestrulae	–	2–3	30
Fenestrula length	1.098±0.146	0.803–1.304	15
Fenestrula width	0.513±0.105	0.305–0.683	15
Trabecula length	0.857±0.282	0.491–1.311	15
Trabecula width	1.070±0.146	0.743–1.221	13
Autozooid length	0.491±0.073	0.378–0.665	17
Autozooid width	0.273±0.045	0.210–0.371	17
Orifice length	0.094±0.015	0.079–0.109	4
Orifice width	0.100±0.012	0.083–0.117	6
Suboral avicularium length	0.041±0.003	0.038–0.046	7
Suboral avicularium width	0.049±0.004	0.041–0.051	15
Frontal avicularium length	0.084±0.014	0.066–0.108	7
Frontal avicularium width	0.053±0.009	0.043–0.063	5
Abfrontal avicularium length/width	0.067±0.002	0.066–0.070	3
Ooecium length (without labellum)	0.214±0.020	0.182–0.231	8
Ooecium width	0.201±0.014	0.175–0.220	7

The primary orifice is semicircular with slightly prominent proximal edge, slightly wider than long (mean size 0.094 x 0.100 mm); the distal margin of the orifice is smooth along its upper edge and with well pronounced denticles along its lower margin; condyles are large and rounded. A pair of oral spines is present, one on each side of the orifice at about mid-length.

The peristome hides the orifice in frontal view and consists of two unequal lobes forming an open sinus (Fig. 2D–F). A single circular avicularium is present on its rim, mid-proximally, 0.041 mm long, proximally directed and oblique to the frontal surface (Fig. 2F).

The avicularium is immersed in the peristome, the avicularian cystid is invisible, and the distal rim of the mandible is finely toothed. Frontal avicularia are sporadic, oval (0.084 x 0.053 mm) demarcated by a raised rim (Fig. 2D, J); the distal margin of the rostrum is smooth, the mandible is semi-oval, the crossbar is complete without columella, and the distal uncalcified area is semicircular. Abfrontal avicularia are small, nearly circular (diameter 0.042 mm); the distal margin of the rostrum is toothed, the mandible is semicircular, and the crossbar is complete without columella.

Ovicells are located above the distal rim of the orifice; ooecia are longer than wide, with an elongate median fissure and a narrow squared labellum; ooecia become partly obscured by secondary calcification in late ontogeny (Fig. 2I).

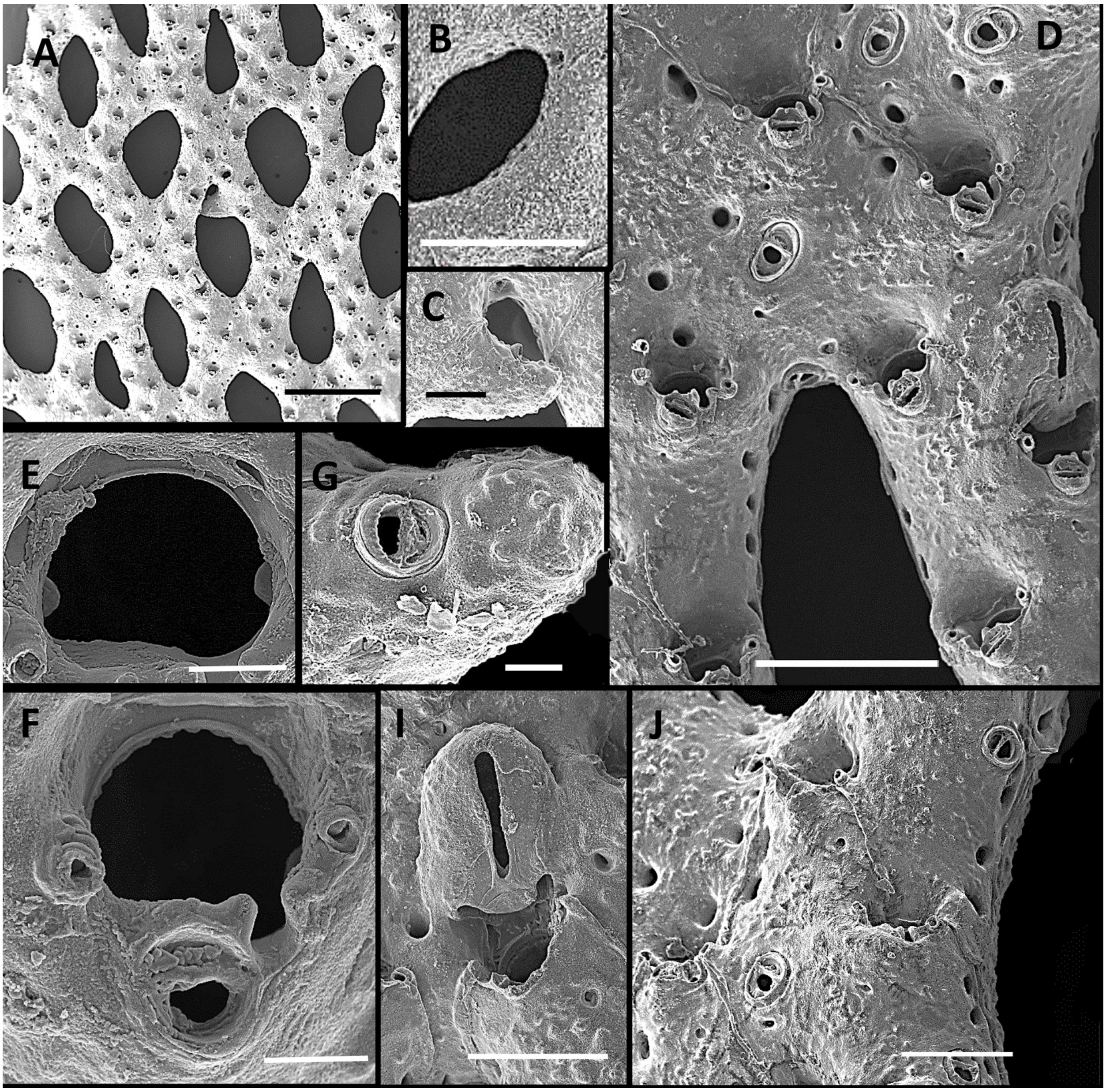

FIGURE 2. *Reteporella obscura* **n. sp.**, holotype, ZIN 1/50742. A. Frontal part of colony; autozooids organized in 2–3 series between fenestrulae. B. Densely granulated abfrontal surface. C. Horn-shaped kenozooid with small avicularium. D. Group of zooids. E. Rounded condyles and denticulation of primary orifice. F. Distal part of orifice, showing denticulate distal margin and the circular, proximo-laterally directed suboral avicularium. G. Abfrontal avicularium. E. Ovicell with well-developed labellum and elongate median fissure. J. Group of zooids. Scale bars: A, B, 1 mm; C, E, F, G, 50 µm; D, 400 µm; I, J, 200 µm.

Remarks. *Reteporella obscura* **n. sp.** was found in the sublittoral zone, at two stations in the Davis Strait of SW Greenland. At first glance, the new species is very similar to *R. beaniana*, which is widely distributed in the Arctic Atlantic, in the appearance of colonies and zooids, in the morphology of the secondary orifice and peristome with widely open pseudosinus, and in having a pair of orificial spines. However, the new species is distinguishable from *R. beaniana* in having a distinct granulation on both surfaces of the colony, and in the shape of the primary orifice which is bell-shaped in *R. beaniana* and semicircular in *R. obscura* **n. sp.** Differences are also observed in the shape of the condyles, which are roundish in the new species and rounded triangular in *R. beaniana* (Hayward & Ryland 1996, 1999). The suboral avicularium of the new species is round with an indistinct cystid, whereas in *R. beaniana* it is oval and the cystid is prominently emerging above the frontal shield. In addition, *Reteporella obscura* **n. sp.** is characterized by globular ovicells, longer than wide with a prominent but relatively narrow labellum, whereas *R. beaniana* has ovicells that are wider than long, and with an arched aperture, and a flattened frontal surface (Hayward & Ryland 1996, 1999).

Distribution. Lower sublittoral zone (165–277 m), Davis Strait (SW of Greenland).

Reteporella vitta n. sp.

(Figs 3, 4; Table 2)

Material examined. Holotype: ZIN 1/50743, one colony; Stn 2016_PA_5_58 (64.8872833251953° N, -34.5760166803996° W; 948 m; T 3.24°C); collected by Alfredo III trawl, MT *Paamiut*, fish-shrimp trawl assessment survey. July 2016.

Diagnosis. *Reteporella* with delicate, reticulate colony, large fenestrulae and dimpled frontal and abfrontal surfaces. Trabeculae long, consisting of one to three alternating series of autozooids without doubling at bifurcations. Autozooids with 1–3 large marginal pores and with wavy edges; primary orifice semicircular, slightly wider than long; condyles large, robust, trapezoidal; spines absent; peristome intermediately tall, consisting of two unequal lobes, often closed forming a roundish spiramen. Circular suboral avicularium with prominent chamber located on larger peristomial lobe; distal rostrum finely denticulate or smooth, crossbar complete, columella absent, palate narrow; frontal avicularia oval with complete crossbar, no columella and narrow palate. Abfrontal avicularia nearly circular, distal rostral margin denticulate, without palate. Ovicells prominent, sometimes with a short labellum and with closed fissure in late ontogeny.

Etymology. Latin "*vitta*" (lacy), alluding to the delicate, graceful, lacy appearance of the colony.

Description. The colony is reticulate, delicate and shiny. The frontal sides of the autozooids face towards the inner side of the rosette, as it is common in *Reteporella* species. As the colony grows, it develops as asymmetrical lateral lobes that curl outwards and backwards, transforming the colony into a funnel, in which, once the lobes come into contact with each other, the abfrontal side becomes the inner surface of the funnel, and the frontal side its outer surface (Fig. 3A, B). The colony is up to 60 x 25 mm in size; the fenestrulae are large, elongate, rhomboidal, polygonal or oval; their length (1.9–2.4 mm) is twice their width (0.7–1.05 mm).

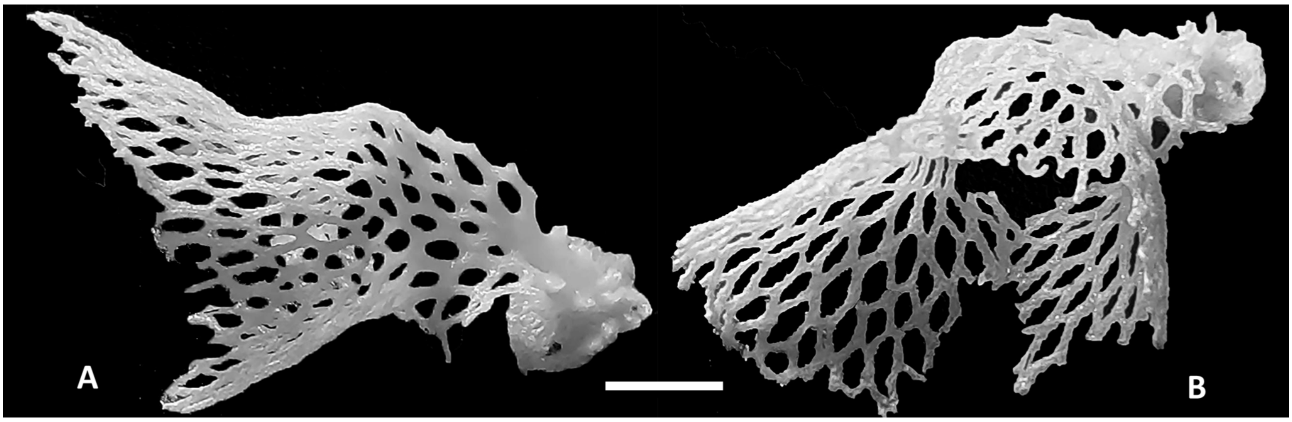

FIGURE 3. General colony view of *Reteporella vitta* **n. sp.**, holotype, ZIN 1/50743. A, Frontal view of colony; B, view into funnel. Scale bar: 5 mm.

Both surfaces of the colony (i.e. zooidal frontal shield and the abfrontal surface) are regularly and densely covered by polygonal depressions marked by thin ridges. The abfrontal side is covered with kenozooids delimited by clearly visible vibices. The trabeculae are long (0.6–1.9 mm) and narrow (0.24–0.65), consisting of 1–3 alternating longitudinal series of autozooids (Fig. 4A, B).

Autozooids are elongate, hexagonal; the frontal shield is shiny and slightly convex with wavy edges delimited by sutures, somewhat blurred in zooids with ovicells (Fig. 4D, E). Autozooids vary considerably in size (Table 2) but they are usually about 0.75–0.85 mm long by about 0.25 mm wide. The dimpled frontal surface bears usually 1–2 large marginal pores, with or without a low rim.

The primary orifice, partly hidden by the peristome, is semicircular, slightly wider (0.12 mm) than long (0.08 mm) (Fig. 4C, D); the proximal edge is straight, the distal margin is smooth along its upper edge, but has a slightly immersed row of minute blunt denticles better pronounced in ovicell-bearing zooids. The condyles are large, blunt, trapezoidal (Fig. 4C), deeply immersed and poorly visible when viewed using a stereomicroscope. Oral spines were not observed in the analyzed specimen.

TABLE 2. Measurements (in mm) of *Reteporella vitta* **n. sp.** (holotype). Abbreviations as in Table 1.

Character measured	Mean ± SD	Range	N
No. zooid rows between fenestrulae	–	1–3	30
Fenestrula length	2.117±0.133	1.946–2.310	10
Fenestrula width	0.888±0.110	0.719–1.047	10
Trabecula length	1.529±0.481	0.593–1.877	9
Trabecula width	0.431±0.118	0.241–0.645	9
Autozooid length	0.648±0.123	0.483–1.040	20
Autozooid width	0.267±0.023	0.226–0.299	20
Primary orifice length	0.085±0.012	0.071–0.102	10
Primary orifice width	0.111±0.005	0.100–0.124	10
Suboral avicularium length	0.047±0.001	0.046–0.049	10
Suboral avicularium width	0.045±0.001	0.043–0.048	10
Frontal avicularium length	0.083±0.015	0.068–0.112	10
Frontal avicularium width	0.056±0.016	0.039–0.082	10
Abfrontal avicularium length/width	0.042±0.007	0.035–0.051	5
Ooecium length	0.235±0.007	0.223–0.243	8
Ooecium width	0.228±0.005	0.219–0.232	8

The peristome hides half of the orifice and consists of two unequal lobes, open or closed, forming in the latter case a small spiramen (Fig. 4C, D), which often disappears due to progressing calcification, regardless of the location of the zooid in the colony.

On the larger peristomial lobe there is a small, rounded (Fig. 4C, D) suboral avicularium (about 0.047 mm in diameter) with a toothed distal rostrum, complete crossbar without columella, the palate as a narrow shelf, and semicircular mandible (Fig. 4D–F). The suboral avicularium is generally oriented proximally and obliquely to the colony surface, and its cystid protrudes noticeably. Frontal avicularia are also small, although slightly larger than the suboral ones, oval, 0.083 x 0.056 mm, parallel to the frontal surface, with smooth rostrum and complete crossbar, palate as a narrow shelf, uncalcified semicircular area proximal to the crossbar often larger than the distal semi-elliptical one, and semicircular mandible (Fig. 4E). Abfrontal avicularia (Fig. 4B) are small, nearly circular (diameter 0.042 mm), with the distal margin of the rostrum toothed, complete crossbar without columella, and semicircular mandible (Fig. 4G).

The ovicell is prominent, the length (0.235 mm) slightly greater than the width (0.228 mm), its proximal surface is slightly flattened, sometimes with a short, weak labellum, but the labellum is usually lacking. The median fissure closes during ovicell formation, leaving in its place a long, narrow median depression in the proximal half of the ooecium (Fig. 4D, E).

Remarks. Despite the large volume of material processed, the new species *R. vitta* **n. sp.** was found only in one sample. The new species has a dimpled surface as *R. watersi* and *R. rara* from the North Atlantic, but in contrast to these species, which have robust colonies and a dull surface (Jullien & Calvet 1903; Hayward 1994; Hayward & Ryland 1996, 1999), the colony of *R. vitta* **n. sp.** is delicate, shiny and with large fenestrulae. Based on the descriptions by Hayward & Ryland (1996, 1999) and Jullien & Calvet (1903), the fenestrulae in *R. vitta* **n. sp.** are 2.3 times larger than those in *R. watersi* and *R. rara*.

The arrangement of autozooids within the colony also differs among these species. In *R. vitta* **n. sp.**, autozooids form a series of 1–3 rows, remaining constant in width at bifurcations, whereas there are 3–5 rows of autozooids in *R. watersi* that double in number at bifurcations.

Reteporella vitta **n. sp.** also differs from *R. watersi* and *R. rara* in the size of autozooids (see Tables 3, 4). For instance, the autozooids in *R. vitta* **n. sp.** are 1.5 times longer than in *R. watersi* and *R.rara.* The primary orifice in all three species is wider than long, but the proportions are different with the primary orifice of *R. vitta* **n. sp.** and *R. watersi* smaller than that of *R. rara* (*c.* 0.137 x 0.2 mm; B. Berning, pers. comm. 2022), in which the proximal edge is slightly more convex than in the new species. The morphology of the condyles differs as well among the three species.

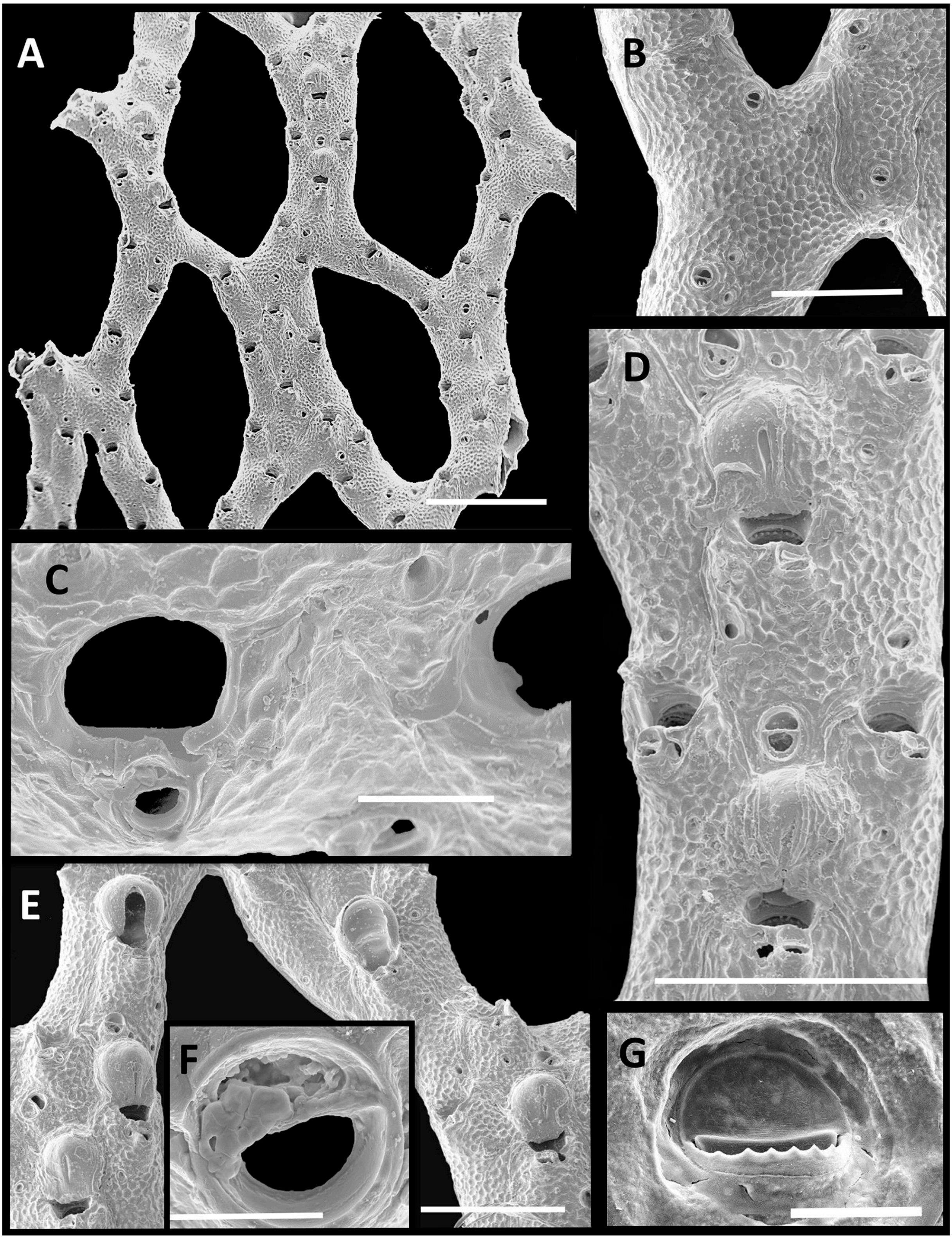

FIGURE 4. *Reteporella vitta* **n. sp.**, holotype, ZIN 1/50743. A. Fragment of colony, frontal surface. B. Abfrontal surface of colony. C. Orifice (condyle visible on the right) and suboral avicularium. D, E. Autozooids with ovicells. F. Frontal view of suboral avicularium. G. Avicularium on the abfrontal surface of colony. Scale bars: A, 1 mm; B, 400 μm; C, 100 μm; D, E, 500 μm; F, G, 50 μm.

TABLE 3. Measurements (in mm) of *R. watersi* (Nordgaard, 1907) from Greenland (this study) and the Faroe archipelago area from Hayward (1994) and Hayward & Ryland (1999). Abbreviations as in Table 1.

Character measured	This study			Faroe Islands
	Mean ± SD	Range	N	Range
No. zooid rows between fenestrulae	–	3–8	15	3–5
Fenestrula length	0.906±0.193	0.484–1.128	15	1
Fenestrula width	0.371±0.148	0.170–0.615	15	0.5
Trabeculae length	1.317±0.429	0.783–2.227	15	–
Trabeculae width	0.763±0.174	0.507–1.059	15	–
Autozoids length	0.442±0.093	0.335–0.747	18	0.45–0.5
Autozooids width	0.318±0.056	0.224–0.421	18	0.25
Orifice length	0.082±0.005	0.079–0.090	10	0.1
Orifice width	0.098±0.004	0.092–0.105	10	0.14
Suboral avicularium length	0.067±0.008	0.082–0.062	15	–
Suboral avicularium width	0.040±0.006	0.030–0.047	15	–
Frontal avicularium length	0.038±0.008	0.025–0.047	10	L > W
Frontal avicularium width	0.028±0.007	0.017–0.038	10	–
Abfrontal avicularium length/width	0.043±0.006	0.033–0.053	12	–
Ooecium length	0.188±0.009	0.160–0.209	5	L > W
Ooecium width	0.176±0.018	0.166–0.192	5	–

Moreover, although all species have a small suboral avicularium, it is oval in *R. watersi* and in *R. rara*, and round in *R. vitta* **n. sp.** The orientation of the peristomial avicularium is also different in the species under consideration; in *R. vitta* **n. sp.** and *R. rara*, it is oriented terminally to the autozooidal surface, while in *R. watersi,* the rostrum is nearly parallel to the frontal autozooidal surface. The location of the suboral avicularium within the peristome also differs in these species. In *R. watersi* and *R. rara* the avicularian chamber is not visible, but in *R. vitta* **n. sp.** it is prominent and clearly raised above the frontal autozooidal surface.

The ooecium of *R. watersi* has an open elongate fissure and a conspicuous labellum, whereas in *R. vitta* **n. sp.** the fissure is closed and the labellum is small or absent. In *R. vitta* **n. sp.**, the ectooecium closes immediately as the ooecium forms, and only an elongate, droplet-shaped depression resembling a fissure is evident on the surface. The ooecium in *R. watersi* has a conspicuous labellum, whereas in *R. vitta* **n. sp.** the labellum is small or absent.

Distribution. Upper continental slope of SE Greenland.

Reteporella watersi **(Nordgaard, 1907)**

(Fig. 5; Table 3)

Retepora beaniana var. *watersi* Nordgaard, 1907: p. 16; Kluge 1962, p. 529, 530, fig. 370.
Reteporella watersi: Hayward 1994: p. 195, fig. 8A, B; Hayward & Ryland 1996: p. 111, fig. 3B; Hayward & Ryland 1999: p. 376, 377, fig. 178A–C.

Material examined. ZIN 4/50741, one colony; Stn 2016_PA_4_40 (61.9967333475749° N; –41.0106666664283° W; 234 m; T 3.9°C); MT *Paamiut*, collected by Alfredo III trawl; fish-shrimp trawl assessment survey. July 2016. ZIN 5/50745, one colony fragment; Stn 2016_PA_1_22 (64.5355499903361° N; – 55.1436500072479° W; 563 m; T 4.12°C); MT *Paamiut*, collected by BEAMTRAWL; fish-shrimp trawl assessment survey. July 2016.

Description. The colony is reticulate, funnel-shaped, thickly calcified, robust and matte, up to 50 x 40 mm in size. The branches consist of 3–5 alternate series of zooids, increasing twice in width at points of fusion. Fenestrulae are relatively small, approximately 0.7–0.9 mm long by 0.2–0.6 mm wide (Fig. 5A; Table 3). The basal surface is covered by kenozooids delimited by prominent vibices (Fig. 5B); the frontal and abfrontal surfaces are deeply pitted with a honeycomb structure.

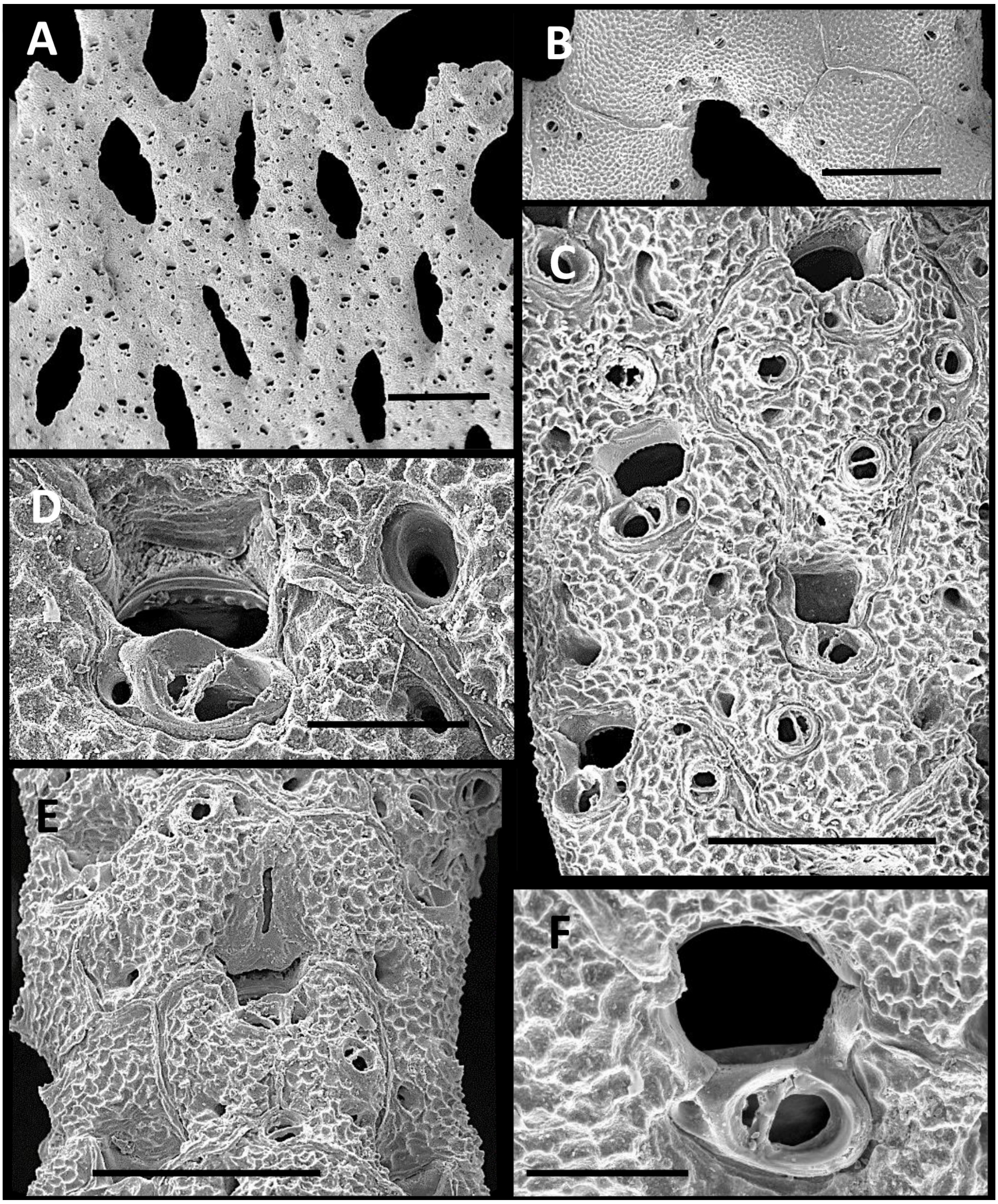

FIGURE 5. *Reteporella watersi* Nordgaard, 1907. ZIN 4/50741. A. Frontal side of colony; autozooids organized in 3–5 series between fenestrulae. B. Abfrontal surface of colony. C. Group of zooids; triangular condyle and denticulation of primary orifice is evident in the autozooid on the bottom left. D. Distal part of zooid, showing denticulate distal margin of orifice and oval, proximolaterally directed suboral avicularium. E. Autozooid with ovicell, which has well-developed labellum and an elongate median fissure. F. Orifice, showing straight proximal margin. Scale bars: A, 1 mm; B, C, E, 300 μm; D, F, 100 μm.

Autozooids (L = 0.35–0.75 mm; W = 0.25–0.42 mm) are located in the inner part of the funnel and delimited by sutures. Several large areolar pores are located near the zooidal margins.

The orifice is wider than long, with a straight proximal margin; the upper distal rim is smooth and with short blunt denticles below (Fig. 5C). The orifice is partly hidden by a peristome, which has two unequal lobes that close to form a circular pseudosinus. The larger lobe bears an oval avicularium directed proximolaterally.

The suboral avicularium is more or less parallel to the zooidal surface with a tall rim, and a few teeth on the distal rostrum; it has a complete crossbar without columella; the palate is a narrow shelf (Fig. 5C, D, F). Oral spines were not observed. The frontal avicularia are slightly smaller than the suboral ones, oval or roundish with complete crossbar and no columella.

The ovicell is immersed, longer than wide, with a pronounced quadrate labellum and an elongate median fissure, mostly covered by pitted extrazooidal calcification during ontogeny (Fig. 5E).

Remarks. The suite of characters observed in *R. watersi*, recently obtained from around Greenland, fits well with previous descriptions of specimens from the Faroe area (cf. Hayward 1994; Hayward & Ryland 1996, 1999). Nevertheless, some discrepancies in skeleton morphology were observed, such as the absence of oral spines in our specimens, which were also lacking in the description by Kluge (1962), as well as in the original description of the species by Nordgaard (1907). The measurements of the specimens analyzed here are also different from those presented in the literature, where zooids and orifices are narrower.

Distribution. Sublittoral, deeper than 200 m in the waters south and northwest of Greenland. Around Faroe Islands at 68 stations, and in Iceland waters at 80 stations, at depths between 210 and 1112 m.

TABLE 4. Summary of the morphological characteristics of the species of *Reteporella* with reticulate colonies and zooids with dimpled surface recorded from the North Atlantic.

Species	Distribution	PO	PO rim (Proximal / Distal)	Spines	Condyles	Peristome
R. rara	N Atlantic	1.5 W>L	C / DD	–	Rh	Low
R. watersi	N Atlantic	W>L	S / VD	+ / –	Tr	QL
***R. vitta* n. sp.**	NW Atlantic	W>L	S / BD	–	Trap	QH

Continued.

Species	Avicularia / avicularian rostrum			Ovicells / Fissure / Labellum	Source
	suboral	frontal	abfrontal		
R. rara	O / RD	C / O	O / C	W=L	Jullien & Calvet 1903
R. watersi	O / SE+FD	C / SC	C	W<L / + / +	Hayward & Ryland 1996; this study
***R. vitta* n. sp.**	C, SE+FD	O+C / SO	C / RD	W=L / + / ±	this study

Abbreviations: Primary orifice (**PO**): wider than long (**W>L**); as long as wide **(W=L)**; straight (**S**); convex (**C**); visible denticulation (**VD**); distinct denticulation (**DD**); smooth edge with one row of blunt denticles behind it (**BD**). Condyles: triangular **(Tr)**; trapezoidal **(Trap)**; roundish, slightly hooked **(Rh)**. Peristome: quite low (**QL**), quite high closing half of PO (**QH**). Avicularium: oval (**O**); circular (**C**); with rough denticles **(RD**); with smooth edge **(SE)**; with fine denticulation **(FD**); rostrum semi-oval (**SO**); semicircular (**SC**). Ovicell: longer than wide (**W<L**). Absent (**–**); present (+); not always present or weakly developed (±).

Discussion

Representatives of the genus *Reteporella* are easily recognized by the distinctive appearance of their colonies, implying that the genus could be well studied not only in the World Ocean (Bock & Gordon 2021), but also in the Arctic region. Indeed, since the second half of the 19th century, records of *R. beaniana* and *R. grimaldii* in the Atlantic Arctic have regularly appeared (i.e. Smitt 1868; Levinsen 1916; Osburn 1919; Kluge 1962). In the 1990s, following the exploration in the 1980s of poorly known areas around the Faroe Islands, it has been established that the diversity of the genus *Reteporella* in the Arctic was higher than previously thought. *Reteporella couchii* and *R. rara*, previously recorded in temperate Atlantic waters, were reported for the first time in the zone of interaction between water masses from the Arctic and Atlantic, and a new species *R. incognita* was also discovered (Hayward 1994; Hayward & Ryland 1996; Klitgaard 1995). However, the record of *R. rara* in the Faroes waters by Klitgaard (1995) seems doubtful given that the species was originally described from the central North Atlantic archipelago of the Azores (Jullien & Calvet 1903), which is located considerably south of the Faroes. The species could have been confused with *R. watersi.*

The processing of new bryozoan samples collected in Greenland waters in 2016 has allowed to establish that the diversity of the genus *Reteporella* in the study area is one of the richest in comparison to other Arctic areas (Kluge 1962; Denisenko 1990; Kuklinski 2009). The present study also states that *R. beaniana* and *R. grimaldii* commonly occur in the study area, suggesting that these species distribution, although common in the Arctic, is limited mainly by spreading of the intermediate Atlantic water masses (Puerta et al. 2020) (Fig. 1).

The intensive sampling undertaken in 2016 indicated that *Reteporella watersi*, which was previously reported from Greenland waters but only northward of 78° N (Koltun 1964; Kuklinski 2009), inhabit also in the southern and western parts of the study area. Frequent records of the species in similar latitudes near Iceland (Hayward *et al.* 2020) and Faroe Islands (Denisenko *et al.* 2016) already suggested that it should also inhabit the southern waters of Greenland. However, in contrast to the neighboring areas, the species occurs less frequently in the study area, where it was found only at three locations (Fig. 1).

The suite of characters observed in *R. watersi* recently obtained from around Greenland fit well with descriptions in some of the latest publications (cf. Hayward 1994; Hayward & Ryland 1996, 1999), but at the same time, there are some discrepancies related to zooidal morphometrics and the absence of proximal oral spines, which were also lacking in specimens described by Nordgaard (1907) and by Kluge (1962). These observations suggest that *R. watersi* is characterized by intraspecific variability within the Arctic as a result of specific environmental differences between typical Arctic areas and areas at the border between the temperate Atlantic and the Arctic, from which the specimens analyzed in previous studies (Hayward 1994; Hayward & Ryland 1996, 1999) were collected.

Based on the distribution of *Reteporella* species in the Arctic, we can speculate that they derive from deep central Atlantic species, analogously to some other predominantly Arctic bryozoan genera, e.g. *Pseudoflustra* (Kuklinski *et al.* 2013). This speculation is supported by the results of studies on population genetics of other Arctic biota, including algae, gastropods and crustaceans (Maggs *et al.* 2008). The spreading of Atlantic species such as *R. beaniana*, *R. grimaldii* and *R. watersi* towards the higher latitudes of the Greenland Sea up to the Arctic Basin took place after the deglaciation of the Arctic about 10,000 years ago. The system of water currents established during that time promoted and supports the bryozoan distribution towards the north, northeast and north-west (Nesis 1983), including the western areas of Greenland.

Based on the results of the present study confirming the existence of new species and new records of *Reteporella* in Greenland waters, we can conclude that the diversity of this group in this area of Arctic is really higher than hitherto recognized (Denisenko & Blicher 2021). Those findings also support our previous conclusion that the fauna of bryozoans in the Arctic as a whole remains underestimated (Denisenko 2020).

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